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FIGURE 6. A brown hyena cub greeting its mother, where sniffing is directed at the anal region.

A COMPARISON OF SOME FEATURES OF THE EVOLUTION, ECOLOGY AND BEHAVIOR OF BLACK AND GRIZZLY/BROWN BEARS

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Abstract. Evolutionary, ecological and behavioral literature is surveyed and related to the adaptive strategy of black and brown bears. A series of hypotheses based on existing data, deduction, inference, and speculation is presented. From an evolutionary perspective black bears are more similar to ancestral forest-dwelling miacids than are brown bears. The brown bear's niche, in contrast with the black bear's, includes more exploitation of open habitat types. Various adaptations of each species to their primary habitat types are discussed. Both species are opportunistic omnivores which have relatively unspecialized guts and ingest high quality food items. When these are not available hibernation occurs. Brown bears are normally 1.5 to 2 times as large as black bears within the same biogeoclimatic zone. This is interpreted in terms of evolutionary history, and habitat preference and productivity. Reproductive rates for both species are low. The reproductive strategy for females of each species involves extended, intensive maternal investment. No paternal investment beyond the copulatory act has been identified. Individuals of both species are somewhat flexible in their use of space for foraging and reproduction, depending upon the distribution of critical resources such as food and mates.

INTRODUCTION

During the past two decades scientists have

received money to study bears because of bears' cultural and economic significance to people. Prior to about 1960 much of our knowledge about bears was inferential and anecdotal. Both the black bear (*Ursus americanus* Pallas) and the brown/grizzly bear (*U. arctos* Linne) seldom occur at population densities greater than one individual per square mile. Because of these relatively low population densities they are seldom seen except at concentrated food sources. Among the most common of these, at least up to a few years ago, were garbage disposal areas (Figure 1). Bears are difficult to locate in natural areas without considerable effort. Since the mid-1950's, however, the private world of bears has become increasingly public. Methods for the capture and recapture of bears have become widely known and used. The use of drugs to either capture or sedate bears has allowed the collection of data on age, weight, reproductive status, anatomy and morphology, and much more (Figure 2).



FIGURE 1. Black bears and attendant at a garbage dump, July, 1968.

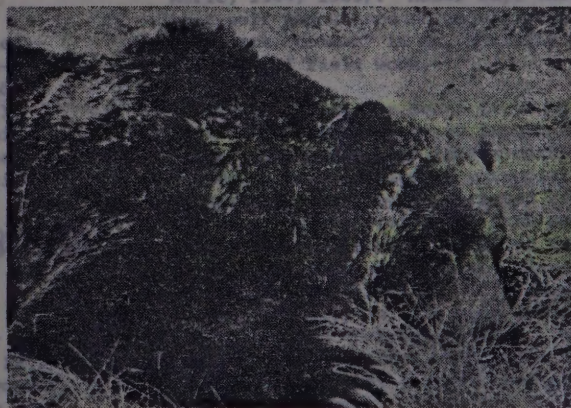


FIGURE 2. Sedated adult male grizzly bear which has been lip-tattooed and weighed and measured as part of an ecological study.

¹ Hereafter referred to as brown bear, but meant to include all North American populations of the species. Where specific reference is made to grizzly bears, this is used to be consistent with an author's original usage.

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The ultimate weapon used by curious humans has been radiotelemetry. With a radio collar around a bear's neck and receivers in peoples' hands, the private world of bears vanished. Radiotelemetry has been particularly valuable in understanding the use of space by bears. In some cases individual black (Rogers, 1976) or grizzly bears (Craighead et al., 1969, 1974) have been monitored for up to seven or eight years and through several reproductive cycles.

The avalanche of scientific research and knowledge related to bears has been documented in the published proceedings of four international conferences on the biology and management of bears (Pearson, 1968; Herrero, 1972a; Pelton et al., 1976; Martinka, in preparation). Despite tremendous advances in knowledge, the state of our understanding of bears is still mainly at the stage of collecting data. The challenge of understanding bears remains great enough at the level of geographically defined populations. For this reason most recent research has contributed towards cataloguing population characteristics within a given geographic area.

So, despite advances in knowledge, integrated theory would be premature. This is true partly because black and brown bears are long-lived species with low reproductive rates. This makes studies having durations of 10 years or more necessary in order to understand important topics such as reproductive strategies and population response to environmental variability. Only one study (Craighead et al., 1974) has thus far extended to this duration. Although data on bear populations have become considerable since 1960, these data are often fragmented and incomplete.

In this paper I summarize important literature and present a series of hypotheses related to the evolution, ecology and behavior of black and brown bears. The areas I will cover are: evolutionary history, food habits, reproductive strategy, and the use of space and its inferred relationship to reproductive strategy.

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EVOLUTIONARY HISTORY

About 25 million years ago, during the early portion of the Miocene, bears appear to have diverged from the *Miacidae* (Colbert, 1955). The *miacids* were a family of small, carnivorous, tree-climbing mammals. The earliest bears were probably forest dwellers like their *miacid* ancestors, although the bears' diets probably included more vegetative items. Bears ultimately became opportunistic omnivores, eating meat when it was easily available and high quality vegetation when it was not. In most areas vegetative food sources are more predictable than are animal food sources. Highly digestible vegetative material came to dominate the diet. Quite late in the bears' evolutionary history species such as *Arctodus* spp., *Ursus arctos* and *U. maritimus* diverged from forest dwelling ancestors and began to utilize the productivity of more open habitat types (Herrero, 1972b). The most recently evolved of these species appear to be the polar bear (*U. maritimus maritimus*), which not only occupies open tundra and ice-covered environments but also has redeveloped the *miacid* habit of being primarily carnivorous instead of following the general

bear strategy of omnivory.

As I infer for their *miacid* ancestors, individual bears of species past and present are solitary except when females are accompanied by young, when family groups sometimes associate, when sibling groups sometimes remain together after weaning, during the breeding season, or at concentrated food sources.

Black bears and brown bears each appear in the fossil record sometime during the mid-Pleistocene. In 1970 I developed a hypothesis which explains some of the differences in adaptive strategy of the two species (Herrero, 1972b). I postulated that the brown bear evolved to exploit the seasonal productivity of non-forested periglacial environments. The productivity of periglacial environments and their influence upon many species of large mammals have been discussed by Geist (1971).

In order for brown bears to exploit the periglacial richness they had to remodel some of their forest adaptations. One of the most important redesigns involved protection of the young. Young bears of both species are sometimes killed by adult bears (Troyer and Hensel, 1962; Hornocker, 1962; Jonkel and Cowan, 1971). Historically they were probably killed by wolves and several other now extinct Pleistocene carnivores. Today in certain relatively complete ecosystems, such as exist in Mt. McKinley National Park, wolves still interact with grizzly bears. Here G. Haber (personal communication) observed wolves inflicting serious injury to a subadult grizzly bear, as well as wolves trying to get at grizzly cubs of the year while the female bear actively defended them (also see Murie, 1944, 1963). Haber says that grizzly bear-wolf encounters at ungulate kills or carrion were "common" in Mt. McKinley during his 10 years of field work.

The potential for death to young or subadults was enough to be an important selection force. The black bear female with young responds to this problem of potential predation by normally foraging in forested regions. Here the cubs receive protection from possible predation by their ability to climb trees (Figure 3). Black bears have short curved claws which appear to aid in tree climbing. This climbing ability is present early in life upon emergence from the winter den (Herrero, 1970a). The cubs climb readily when presented with unfamiliar stimuli. In this manner they protect themselves from potential predators. To protect her genetic investment, the female needs only to wait nearby or to threaten and chase off potential predators (Figure 4). She does not need to engage potential predators directly; indeed, to do so might result in injury to her and thus reduce her reproductive fitness.

The brown bear by contrast has a different strategy of cub protection. Basically it is a forest bear remodelled to exploit the seasonal productivity of periglacial edges. Today and historically, similar open habitat types are or were found in tundra, grasslands, alpine and subalpine zones, and along oceans, bays, and rivers. The brown bear has not lost its ability to forage on the forest floor, but it gained the ability to exploit open habitat types at their peaks of productivity (Figures 5 and 6). The brown bear has evolved certain characteristics in response to its periodic utilization of open

habitat types. Females can defend their cubs in areas where trees do not exist. I hypothesize that they do this by being more aggressive toward conspecifics than are black bear females, especially to certain males, as well as toward other potential predators, including man. This characteristic has allowed them to exploit open habitats, but often places them in conflict with people (Herrero, 1970b, c, 1976).



FIGURE 3. Black bear cub of year climbing a tree.

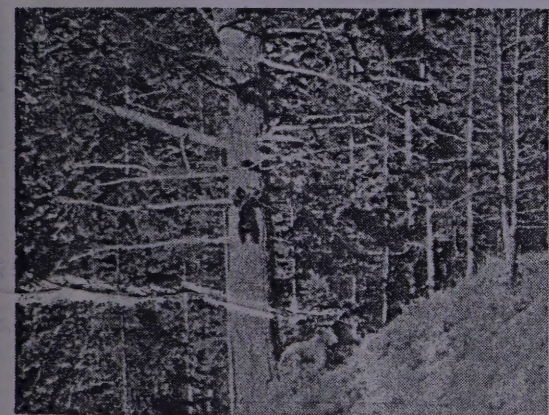


FIGURE 4. Blond color phase black bear female waits at base of tree. The female and her cub were startled by people.

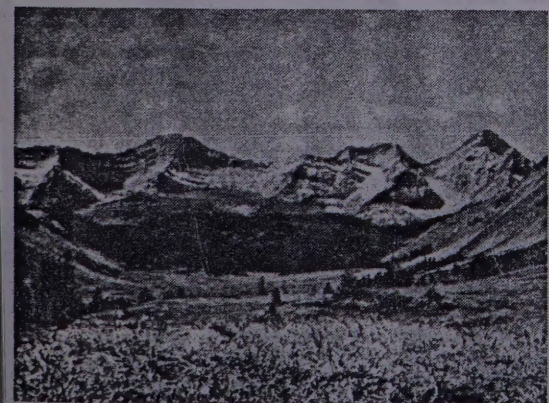


FIGURE 5. Sub-alpine meadow grizzly bear habitat in Banff National Park, Canada.

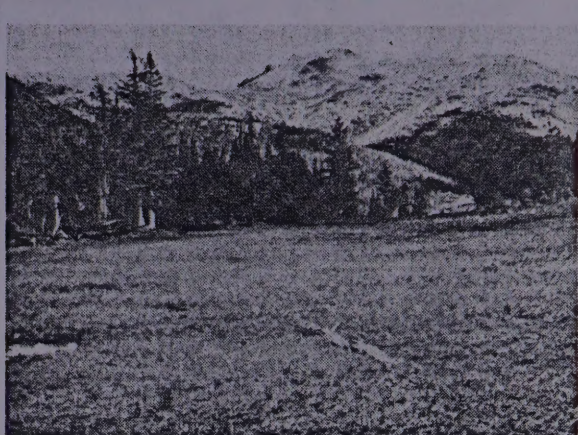


FIGURE 6. Sub-alpine wet meadow grizzly bear summer habitat in Banff National Park, Canada.

Brown bears, when compared to black bears, show other adaptations related to use of open habitat. They have longer front claws which, combined with a larger shoulder and back muscle mass, makes them rapid diggers. Perhaps these features adapted them to exploit ground dwelling rodent populations found in many types of open habitat. The distribution of brown bears was historically quite similar to that of ground squirrels (Banfield, 1964). In at least one area, the Tuktoyaktuk Peninsula in northern Canada, ground squirrels form an important component of the diet today (R. Russell, personal communication). The long claws and digging ability are also advantageous when exploiting other ground-dwelling rodents, and also roots, bulbs, corms, and tubers.

Another brown bear characteristic, when compared to black bears in the same biogeoclimatic zone, is that individuals of the same age-sex class are larger, normally by a factor of 1.5 to 2. (Data are surprisingly lacking, but I compared the data of K. Greer [personal communication] with Barnes, 1967.) Once able to exploit the productivity of open and forested areas, the evolution of brown bears was in many ways shaped by the nature of the productivity of these environments. As the glaciers retreated brown bears repeatedly moved into unexploited periglacial areas of seasonally abundant vegetative forage. Here the diet also probably contained ungulate carrion or fresh-killed ungulates, as well as ground-dwelling rodents. Under these conditions I would expect the highest possible reproduction rates, and the birth of large and vigorous young (Geist, 1971; Rogers, 1976). With abundant food the cubs could grow rapidly and attain large body sizes.

In summary the black bear is more like the typical ancestral bear—a primarily forest adapted form. Digestively it can utilize the foods of open areas, but behaviorally and anatomically it is more adapted to the forest. The North American brown bear, on the other hand, does not forage by climbing trees for mast and fruits as do black bears in some areas (Pelton and Burghardt, 1976), but otherwise it can utilize high quality plant and animal foods in the forest. Brown bears, more so than black bears, also venture into open areas to forage.

Both species throughout all but the southernmost parts of their range face periodic food

shortage during winter. They each respond to this by hibernation (Folk et al., 1972, 1977).

FOOD HABITS

The distribution and abundance of high quality food items influenced the evolutionary divergence between black and brown bears, as well as the ecology and behavior of each species. The availability of food also appears to directly control the reproductive success of black bears from year to year (Jonkel and Cowan, 1971; Rogers, 1976). It is reasonable to postulate that the same controls operate for brown bears, although this has not been demonstrated. The fact that vegetative foods do not escape, and a lack of predator pressure except on females with young, helps to explain the often solitary foraging behavior of individuals of each species. There appear to be no food resources which individual black or brown bears can better exploit cooperatively in groups. Occasionally, however, food items occur in such an abundance that many conspecifics, and sometimes bears of both species, will congregate together to feed (Hornocker, 1962; Stonorov and Stokes, 1972; Martinka, 1973; Rogers, 1977).

Food is a critical resource, sometimes in short supply because of environmental variability. A basic understanding of food habits is therefore essential to understand the ecology and behavior of each species.

Both black and brown bears are omnivorous, which does not mean that they will eat anything. They have relatively unspecialized digestive systems—essentially a carnivore's digestive system which has been lengthened (Davis, 1964), probably to allow for better digestion and absorption of vegetative matter. They have no cecum and their stomachs are too acidic to support the microflora and microfauna needed for digestion of cellulose (Rogers, 1976). Therefore, they cannot, or can only very poorly, digest the structural components of plants (Mealey, 1975). They are not ruminants, but each species of bear can survive on diets of 95% and more vegetative matter (for example, see: Mundy, 1963; Poelker and Hartwell, 1973; and Hamer, 1974). They do this by maximizing the quality of the food items ingested; for example, choosing items which can be digested by their simple guts. Given this constraint both species are digestively flexible. Starch, sugar from berries and other fruits, animal and plant protein, as well as most animal and plant storage fats, are all digested (Mealey, 1975). The proportions of each in the diet vary greatly from area to area or seasonally (Mealey, 1975, and compare Tisch, 1961, with Pelton and Burghardt, 1976, and with Poelker and Hartwell, 1973).

The digestibility of plant protein has been studied in grizzly bears by Mealey (1975). Plant protein from succulent herbs appeared to be about 43% digestible as compared to about 78% digestibility for animal protein and fat sources. Starch was about 79% digestible; sugar from berries and other fruits was assumed to be highly digestible. Digestibility of food items by black bears has not been studied but could be expected to be similar, though perhaps less efficient with regard to digestibility of plant protein. The grizzly compared

to the black bear may have a longer gut (Mealey, 1975).

The ability to digest a wide range of food items is related to the omnivorous diet of each species. Individuals of each species appear to prefer the most digestible energy and nutrient-rich food items which are economically available at a given time. When plant protein is a major item in the diet its relatively low digestibility is counterbalanced by large intake.

Selection for micronutrients is as yet unstudied. With the possible exception of selection for micronutrient needs, both species of bears appear to try to maximize the intake of high quality food items such as: animal tissue, roots, bulbs, tubers, corms, berries, other fruits, mast, and certain grasses, sedges and forbs. Green plant tissue appears to be ingested by grizzly bears mainly during its phenological periods of high protein content and low presence of structural materials such as cellulose (Mealey, 1975). Other things being equal, high plant protein sources appear to be preferred over low plant protein sources. The same general model probably also applies to black bears.

Because of its claws and musculature, the brown bear is more able to exploit food items which occur in the soil and must be dug (Figures 7 and 8). The black bear being the more adept climber can more effectively forage for mast where it occurs and when it is still on trees (Pelton and Burghardt, 1976). For the most part, there appears to be a great deal of potential food item overlap between the species. In areas of sympatry brown bears appear to have a competitive advantage over black bears in open habitat types (Shaffer, 1971) (Figure 9). I relate this to the former's evolutionary history, especially their aggressive defense of young and their average larger body sizes.



FIGURE 7. A startled adult female grizzly bear. Note the long front claws.

In general, the body weights attained by individuals of each species reflect the productivity of the ecosystems where they forage. Within a given geographic area such as the so-called Yellowstone ecosystem, similar age-sex grizzly bears are roughly 1.5 to 2 times larger than black bears (compare the data of Greer [personal communication] with Barnes, 1967). Black bears in productive food areas such as Michigan (Erickson et al., 1964) may have average

weights almost equivalent to weights of grizzly bears found in food-poor areas such as the interior Yukon Territory (Pearson, 1975).



FIGURE 8. Extensive grizzly bear diggings for the roots of *Hedysarum* spp., Banff National Park, Canada.



FIGURE 9. Adult female grizzly bear with older offspring travelling through a sub-alpine glade.

Many aspects of the ecology and behavior of bears can be understood by reference to the foraging strategy of each species. I shall try to treat two topics from this perspective: firstly, reproductive strategy, and secondly, the use of space and its relationship to reproductive strategy.

REPRODUCTIVE STRATEGY

Both black and brown bears have low reproductive rates. It is commonly believed that where both species occur within the same biogeoclimatic zone black bears have a significantly higher reproductive rate. Evidence for this view is largely inferential and incomplete. Detailed population and reproductive studies have not been carried out where both species occur in the same region.

An understanding of reproductive rates is fundamental for management of a bear population. It is also essential for understanding the reproductive strategy of males and females of a species. For bears, reproductive rate

can be calculated by taking the average number of cubs produced per adult female per year and dividing this by the average length of the reproductive cycle (Craighead et al., 1974). To calculate reproductive rate one has to know three parameters for a population: average age of first reproduction, average litter size, and average duration between litters. Each of these reproductive parameters has been shown to vary in response to ecosystem productivity, both from year to year and from area to area. Certain parameters would be expected to vary with hunting pressure and, in general, with the numerical status of the population. These points will subsequently be documented and discussed. They are pointed out here because they help to identify the difficulties in determining reproductive rates. What is required are detailed long-term or cross-sectional population and reproductive studies within a given area.

Only one study of one species thoroughly meets these criteria. Craighead et al. (1974) report an average reproduction rate of 0.658 and an average reproductive cycle of 3.40 years for 30 grizzly bear females in Yellowstone National Park. Reproductive rates have also been calculated for black bears in Idaho: 0.782 (Reynolds and Beecham, 1977), and Oregon: 1.07 (Lindzey, 1976). Calculation of black bear reproductive rates was based upon a small sample (5 females) in the Reynolds and Beecham study. Lindzey's work used a large cross-sectional sample (242 females collected by hunters over a three-year period). This contrasts with the Craighead et al. (1974) approach where a much smaller number of individually identified females had their reproductive histories studied longitudinally. Both the cross-sectional and longitudinal approaches should work equally well; however, a longitudinal study would better represent the influence of year-to-year environmental variability and population number variability on reproductive rate. Unfortunately, we cannot directly compare the figures of Craighead et al. (1974) with Lindzey (1976) because they were calculated in different biogeoclimatic zones; and the Lindzey population was fairly heavily hunted as compared to the Craighead et al. population which occurred mainly in an unhunted national park. The figures derived by Craighead et al. (1974) and Lindzey (1976) will help to establish the range of variability of reproductive rate after other studies are completed.

Table 1 briefly details the key reproductive parameters found by various workers throughout North America. I have only included results from major studies, and normally only those results based upon population studies of known-age individuals.

Some conclusions which seem merited from consideration of these are: 1) age of first parturition and duration of reproductive cycle are quite variable for each species; 2) the average number of offspring varies within a small range from one biogeoclimatic zone to another for a given species (although standard deviations were seldom available, sample sizes were commonly large and differences were probably significant); and, 3) productivity for black bear and brown bear populations cannot yet be validly compared.

TABLE 1. Reproductive Data From Adult Female Black and Brown Bears

BLACK BEARS

Mean litter size (#), mean placental scar rate (*), mean number of corpora lutea (+)		Hunted (X) or for the most part unhunted ()	Studied by	Where studied
2.05 #		X	Erickson et al. (1964)	Michigan & Alaska
1.65 #		X	Jonkel & Cowan (1971)	Montana
1.88 *		X	Poelker & Hartwell (1973)	Washington
2.29 + (for females 5 yrs. & older)		X	Lindzey (1976)	Oregon
1.9 #		X (heavily hunted, at least prior to study)	Reynolds & Beecham (1977)	Idaho
Age of 1st estrus	Age of 1st reproduction			
3.5	-	X	Erickson et al. (1964)	Michigan & Alaska
4.5	1st cubs in a sample of 3 females not conceived until 6.5, 7.5 & 8.5 yrs.	X	Jonkel & Cowan (1971)	Montana
	Successful breeding by 3.5 yrs. for some individuals. Sexual maturity in 44% by their 4th summer; all by 5th summer.	X	Poelker & Hartwell (1973)	Washington
	Most, if not all, 5 yr. old females had been pregnant either as 3 or 4 yr. olds.	X	Lindzey (1976)	Oregon
	First breeding, 3.5 yrs. (N=3), 4.5 yrs. (N=5), 5.5 yrs. (N=1)	X (see prior reference)	Reynolds & Beecham (1977)	Idaho
	80% bred at 3.5 yrs.	?	Collins (1973)--as cited in Reynolds & Beecham (1977)	North Carolina
Frequency of litters				
2 females had 2 litters each with in a 3 yr. period. 9 others had no litters for at least 2 conse- cutive years, and 2 skipped 3 yrs.		X	Jonkel & Cowan (1971)	Montana
"Corrected" lactation rate of 19% and estrus rate of 31%		X	Poelker & Hartwell (1973)	Washington
Mean litter frequency of 31% (for 3 yrs.)		X (see prior reference)	Reynolds & Beecham (1977)	Idaho
Reproductive rate				
1.07 for females 5 yrs. and older based on corpora lutea counts; however, 3 and 4 yr. old females had lower repro- ductive rates.		X	Lindzey (1976)	
0.782 based on 5 reproductive cycles of 4 females		X (see prior reference)	Reynolds & Beecham (1977)	

TABLE 1 (Cont.)

BROWN BEARS

Mean litter size	Hunted (X) or for the most part unhunted (0)	Studied by	Where studied
2.36	X	Troyer & Hensel (1964)	Alaska (Kodiak National Wildlife Refuge)
2.33	X	Hensel et al. (1969)	Alaska Peninsula
1.7	0	Martinka (1971)	Montana (Glacier Na- tional Park)
2.0	0	Mundy & Flook (1973)	British Columbia (Glacier National Park)
1.75-2.50	0	Craighead et al. (1974)	Wyoming (Yellowstone National Park)
1.7	0	Pearson (1975)	Yukon Territory (Kluane National Park)

Age of 1st estrus	Age of 1st reproduction			
3-6; usually at 4	3 for some females	X	Troyer & Hensel (1964)	Alaska (Kodiak National Wildlife Refuge)
4.5	7 had 1st litters at 5, 2 at 6 yrs., 4 at 7 yrs. and one each at 8 & 9	0	Craighead et al. (1969)	Wyoming (Yellowstone National Park)
6.5	3 first bred at 6.5, 3 others at 7.5, one at 8.5	0	Pearson (1975)	Yukon Territory (Kluane National Park)

Frequency of litters				
Normally bred at 3 yr. intervals	X	Hensel et al. (1969)	Alaska Peninsula	
Reproductive cycle of individual females varied from 2-7 yrs. Mean reproductive cycle was 3.40 yrs.	0	Craighead et al. (1974)	Wyoming (Yellowstone National Park)	
Normal interval between litters at least 3 yrs.	0	Pearson (1975)	Yukon Territory (Kluane National Park)	

Reproductive rate 0.658	0	Craighead et al. (1969)	Wyoming (Yellowstone National Park)	
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The main environmental variable which has been identified as influencing reproductive output is the nutritional status of the female during the fall. Jonkel and Cowan (1971) were the first to convincingly correlate low reproductive output with major food crop failure for black bears. Rogers (1976), working with the same species, has convincingly documented a more general hypothesis linking reproductive output to nutritional status of the female. Rogers found that only females able to attain a certain weight in fall gave birth in spring. Postconception food crop failure appeared to induce some form of abortion in already impregnated females. Bears have delayed implantation of the fertilized embryo. This gives them what seems to me to be an opportunity for

energetically inexpensive abortion. I suspect, although it has not been demonstrated, that pregnant female brown bears respond to nutritional status in the same manner. Rogers' work on black bears also showed that high calorie intakes during captivity or at rich food sites such as dumps advanced the age of sexual maturity by almost two years.

Nutrition is also suggested as a major variable influencing reproduction when productivity for the same species is compared across different biogeoclimatic zones. Several studies suggest that black bear populations have the highest productivity in the eastern United States where mast is a normal and energy-rich component of the diet (Spencer, 1955; Harlow, 1961; Stickley, 13

1961; Erickson et al., 1964; Collins, 1973; Rogers, 1977). Collins (1973), for example, found in North Carolina that 80% of the females first breed by 3.5 years. Generally, black bears in the eastern USA appear to have a lower minimum breeding age, higher inferred reproductive rates, and heavier body weights. Similarly, coastal areas (Poelker and Hartwell, 1973; Lindzey, 1976) appear to allow for higher inferred reproductive rates than do interior areas with continental climates (Jonkel and Cowan, 1971; Reynolds and Beecham, 1977). This last comparison, coastal versus continental area population productivity, can also be made for brown bear populations (Troyer and Hensel, 1964; Hensel et al., 1969, for coastal populations; Craighead et al., 1974; Pearson, 1975, for interior populations), and it shows the same trend.

Hunting by man probably is an important variable influencing population structure and probably influencing reproductive output via parameters such as the quality of vacant habitat and the social aspects of intraspecific competition. Intensity of hunting has not been clearly documented in any studies.

I conclude that reproductive data for black and brown bear populations have major limitations which inhibit further insight which might be gained by comparing the reproductive ability of the two species. (This contradicts Herrero [1977] who, based on more superficial examination of data, reached different conclusions.)

The conclusion that each species has a low reproductive rate is valid. Related to this, each species has a high maternal investment in care of offspring. Once the cubs are born the female attempts to maximize her reproductive fitness by intensive care and education of offspring. Defense of young has been discussed and is an important dimension of the female's maternal investment. Exactly what cubs learn from females has not been studied except anecdotally by Krott and Krott (1962). Casual observation suggests that cubs at least learn considerable information related to suitable food items and their seasonal occurrence.

Young male offspring normally disperse from the female's home range; but young females may remain, eventually being incorporated into the home range of the adult female (Jonkel and Cowan, 1971; Pearson, 1975; Rogers, 1976). Rogers (1976) implies that adult females may try to expand their own home range in order to accommodate some of their female offspring. Adult female bears thus invest heavily in their offspring.

Regarding the reproductive strategy of adult females of both species, the individual female's reproductive fitness would be maximized by choosing to mate with the "best" male (a male bear whose inclusive genetic fitness is highest). It appears, however, that males do the choosing. Grizzly bear males become especially aggressive during the breeding season and larger, more aggressive males normally dominate smaller individuals (Hornocker, 1962). Both species are sexually dimorphic and males are about 1.5 times larger than females (Jonkel and Cowan, 1971; Pearson, 1975). It is appealing to assume that larger, dominant individual males do much of the breeding, and that there

is strong selection pressure for large, aggressive males. Data are lacking, but both sexes of both species can be promiscuous; therefore, it is possible for one male to mate with several females. Whether a female can be impregnated by more than one male is unknown. Poelker and Hartwell (1973) consider it unlikely that females are polyandrous, but Rogers (1977) considers to be likely. Craighead et al. (1969) observed female grizzly bears copulating with one or two males in one day, and up to four different males in one season.

Males of both species appear to compete with one another for mates and to attempt to maximize their fitness by copulating with as many females as is possible. Spermatogenic activity in males has been shown to precede as well as exceed the period of receptivity in females (Erickson et al., 1964; Poelker and Hartwell, 1973; Pearson, 1975). The number of females which a male can mate is probably influenced by variables such as population density and distribution during the mating season. For example, the Craigheads (Craighead et al., 1969) found that adult grizzly bears of each sex were promiscuous near concentrated food sources such as dumps. By contrast, we (Herrero and Hamer, 1977) observed one male grizzly bear which isolated a single female on top of a mountain for two weeks. She copulated with the male at the end of this period. Both male and female grizzly bears therefore appear to have flexible reproductive strategies, depending perhaps upon population density and the probability of finding a mate. The area where we observed the isolation of the female was one of low population density compared to Yellowstone near the dumps. Even the most aggressive male at Yellowstone had trouble isolating and defending a female (Hornocker, 1962); it would not appear to be to the male's advantage to do so under these conditions. Whether males are able to select for female quality is unknown.

Given a flexible strategy with respect to the degree of isolation and defense of females versus the extent of promiscuity, we can still ask what makes a reproductively successful male. I speculate that, for both species, the successful male is aggressive enough, coupled with his size, to be able to dominate other males, and use his social status to gain access to reproductively ready females. He also wanders far enough during the breeding season to be able to locate females, primarily, I assume, by their scent.

A possible aspect of the male's reproductive strategy is infanticide: some males may occasionally kill cubs (Troyer and Hensel, 1962; Hornocker, 1962; Jonkel and Cowan, 1971; also, see Kemp, 1976). We do not know who kills whom, but it is consistent with evolutionary theory to assume that males will not kill their own offspring and will have evolved some means of preferentially killing the offspring of other males. This has been well documented for other species such as lions and langurs (Sugiyama, 1967; Schaller, 1972; Eisenberg et al., 1972; Bertram, 1975).

THE USE OF SPACE AND ITS INFERRED RELATIONSHIP TO REPRODUCTIVE STRATEGY

Understanding the use of space by bears is where radiotelemetry has paid the greatest dividends. I summarize what is known about the use of space and then relate information about the

use of space to the concept of reproductive strategy:

1. Home range use is primarily influenced by food quality, availability, and distribution (Stickley, 1961; Hatler, 1966; Jonkel and Cowan, 1971; Amstrup and Beecham, 1976; Reynolds and Beecham, 1977; Craighead, 1977).

2. For each species, adult males have home ranges two to four or more times as large as those of adult females. Adult male home ranges overlap the home ranges of several females (Jonkel and Cowan, 1971; Poelker and Hartwell, 1973; Pearson, 1975; Amstrup and Beecham, 1976; Lindzey, 1976; Reynolds and Beecham, 1977).

3. Home ranges of adult males commonly overlap, but at least in some areas a major core portion of adult female home ranges are mutually exclusive. Some have argued that females can be territorial (Jonkel and Cowan, 1971; Pearson, 1975; Rogers, 1976). Lindzey (1976) relates spatial and temporal separation of adult female black bears to linear dominance relationships. He also postulates that cases of overlapping home range may be explained by the relatedness of individuals whose home ranges overlap. Reynolds and Beecham (1977) argue convincingly that adult female black bears are not territorial and they explain the lack of overlap of core home range areas as being due to mutual avoidance behavior at home range boundaries, which would contrast with active defense of a territory. In at least one study of grizzly bears home ranges of both males and females were shown to have significant overlap (Craighead, 1977). Despite the evidence which demonstrates significant spatial and temporal separation of female bears in most biogeoclimatic zones, there are still occasional seasonal concentrations of bears of each species and both sexes at major food sources such as salmon streams, garbage dumps, or extensive berry patches. Here hierarchical relationships appear to exist (Stonorov and Stokes, 1972; Rogers, 1977).

Both species of bears appear to be somewhat socially flexible in the use of space, the system of spacing chosen being related to relative evenness versus concentration of food and to the defendable nature of a food source. Because of their smaller home ranges, females are more apt to utilize a type of spatial and temporal isolation having little overlap.

4. The size of the home range for an individual of a given age-sex class appears to be related to how seasonally complete and productive the environment is with regard to food. This point is more clearly demonstrated for brown bears than for black bears. In interior areas such as the Yukon Territory west of the St. Elias range and in Yellowstone National Park, brown bear foods are relatively dispersed in time and space, which results in large home ranges. In coastal Alaska, however, home ranges are smaller, presumably because all brown bear forage requirements can be met within significantly smaller areas (Berns et al., 1977; Atwell et al., 1977). The degree of spatial and temporal isolation of individuals has not yet been reported for these coastal Alaska populations. Work needs to be

done to quantify the food productivity of different areas for each species and its relationship to the use of space by individual age-sex classes.

5. Within a given geographic area where black bears and brown bears are sympatric, brown bears normally have significantly larger home ranges than do black bears (compare the data of Craighead, 1977, to that of Barnes, 1967, for Yellowstone). This may reflect the greater energy needs of the larger brown bear, as well as the brown bear's ability to exploit both open as well as forested areas. The brown bear moves freely from one highly productive site to another and is outcompeted only by people. In open areas the black bear normally (but not always) defers to both brown bear and man (Barnes, 1967; Shaffer, 1971).

6. Home range size and location for adult black bears can be dynamic. Alt (1977) reports changes in home range size related to reproductive status, and especially with regard to the seasonal development and distribution of food sources. Reynolds and Beecham (1977), also with black bears, found that for adult males the annual center of home range location varied significantly between years. However, others have shown stability of home range locations (Jonkel and Cowan, 1971; Amstrup and Beecham, 1976). Again, flexibility in the use of space is suggested. A similar flexibility in the use of space probably also exists for brown bears. The controlling variable appears to be the quality, distribution, and abundance of food items.

Points one through six can be interpreted as showing that the use of space is a central element in the foraging strategy of both species of bears and for both sexes. Combining this information with points previously raised, space appears to be used by bears of each species in order to gain access to at least three critical resources: food, mates, and a relatively safe area where females raise offspring. Each variable is a key component of reproductive strategy.

The female's reproductive success appears to be related to her level of nutrition. The value of a productive home range is therefore expressed in the death or life of offspring. After weaning, the reproductive success of at least the female offspring appears to sometimes be related to the mother assisting the offspring to establish a home range adjacent to and partly including that of the mother. The female's smaller home range, as compared to that of males', appears to require her to forage more intensively than do males. This is based on the assumption that, despite her smaller body size, her energy needs are high during lactation; and at other times she shares food with offspring. Her smaller home range may respond to certain needs related to cub care. It likely means that during the breeding season males must find females rather than the converse.

Pearson (1975) found that shortly after emergence from hibernation females with young will go to high altitude areas where little forage exists. He interpreted this as possibly being related to protection of the offspring from marauding males. Possible spatial isolation of females with young from adult males has not been reported for black bears or, by others, for brown bears.

The home ranges of mature males of each species normally overlap those of three or more females. This appears to allow the males access to several potential mates. Despite extensive home range overlap of adult males, they still must compete, possibly including infanticide. Kemp (1976) found that when mature adult black bear males were removed from a population, within two years the population size and density doubled. It subsequently began a decline, supposedly returning toward original carrying capacity as immature males became mature. It appears that dispersing subadult males move until they find unoccupied habitat, or habitat for which they can successfully compete.

We may now have further insight as to why bears of both species are relatively solitary. Except when engaging in courtship and copulation, or when females are with young, or when some siblings remain together after weaning (as a social unit they have increased safety and status and hence foraging ability), or when attracted to concentrated food sources, individuals of each species of bear can most effectively forage when solitary. There is no advantage conferred to larger groups either for foraging, mating, or in the protection of young. One exception may be occasional alliances of several female bears and their offspring (Murie, 1944, 1963; Craighead et al., 1969; G. Haber, personal communication), which could offer better protection against marauding male bears.

In bears, and all species, sociality and other behavior have been molded by ecological opportunity interacting with the genetic makeup of ancestral species. The manner in which individuals of a bear population exploit a given biogeoclimatic zone has been shown to be somewhat flexible and to depend primarily on spacial and temporal distribution of resources, and the constraints and patterns imposed by the evolutionary history of the species. This flexibility goes much further than I have here been able to discuss. It extends to the level of the individual bear, each of which has certain idiosyncracies in the manner in which it exploits resources and attempts to propagate its genes.

LITERATURE CITED

- Alt, G. L. 1977. Dynamics of home range and movements of black bears in Northeastern Pennsylvania. Paper delivered to Fourth International Conference on Bear Research and Management, Feb. 21-24, Kalispell, Montana.
- Amstrup, S. C., and J. Beecham. 1976. Activity patterns of radio-collared black bears in Idaho. *Journal of Wildlife Management* 40(2): 340-348.
- Atwell, G., D. L. Boone, J. Gustafson, and V. D. Berns. 1977. Brown bear summer alpine habitat requirements on the Kodiak National Wildlife Refuge. Paper delivered to Fourth International Conference on Bear Research and Management, Feb. 21-24, Kalispell, Montana.
- Banfield, A. W. F. 1964. Grizzly territory: Exact range of arctic bears is obscured by old rumors. *Natural History* 73(3): 22-27.
- Barnes, V. G. 1967. Activities of black bears in Yellowstone National Park. MSc Thesis, Colorado State University, Fort Collins.
- Berns, V. D., G. C. Atwell, and D. L. Boone. 1977. Fall brown bear habitat use and movements at Karluk Lake on Kodiak Island. Paper delivered to Fourth International Conference on Bear Research and Management, Feb. 21-24, Kalispell, Montana.
- Bertram, B. C. R. 1975. The social system of lions. *Scientific American* May: 54-65.
- Colbert, E. H. 1955. *Evolution of the Vertebrates*. John Wiley and Sons, New York.
- Craighead, J. J. 1977. Critical habitat concept as applied to grizzly bears. Paper delivered to Fourth International Conference on Bear Research and Management, Feb. 21-24, Kalispell, Montana.
- Craighead, J. J., M. G. Hornocker, and F. C. Craighead. 1969. Reproductive biology of young female grizzly bears. *Journal of Reproduction and Fertility* Supplement 6: 447-475.
- Craighead, J. J., J. R. Varney, and F. C. Craighead. 1974. A population analysis of the Yellowstone grizzly bears. *Montana Forest & Conservation Experiment Station, University of Montana, Missoula* 40: 20 pp.
- Davis, D. D. 1964. The giant panda, a morphological study of evolutionary mechanisms. *Chicago Natural History Museum, Fieldiana Zool. Mem.* 3: 339 pp.
- Eisenberg, J. F., N. A. Muckenhirn, and R. Rudran. 1972. The relation between ecology and social structure in primates. *Science* 176: 863-874.
- Erickson, A. W., J. Nellor, and G. A. Petrides. 1964. The black bear in Michigan. *Agricultural Experimental Station, Michigan State University, East Lansing, Research Bulletin* 4.
- Folk, G. E., M. A. Folk, and J. J. Minor. 1972. Physiological condition of three species of bears in winter dens. Pp. 107-124, In: S. Herrero (Ed.), *Bears--Their Biology and Management*, New Series #23, International Union for Conservation of Nature, Morges, Switzerland.
- Folk, G. E., J. M. Hunt, and M. A. Folk. 1977. Hibernating bears: Further evidence and bioenergetics. Paper delivered to Fourth International Conference on Bear Research and Management, Feb. 21-24, Kalispell, Montana.
- Geist, V. 1971. *Mountain Sheep: A Study in Behavior and Evolution*. University of Chicago Press.
- Hamer, D. 1974. Distribution, abundance, and management implications of the grizzly bear and mountain caribou in the Mountain Creek Watershed of Glacier National Park, B.C. MSc Thesis, University of Calgary.
- Hensel, R. J., W. A. Troyer, and A. W. Erickson. 1969. Reproduction in the female brown bear. *Journal of Wildlife Management* 33(2): 357-365.
- Herrero, S. 1970a. A black bear and her cub. *Animals* 12(10): 444-447.
- Herrero, S. 1970b. Human injury inflicted by grizzly bears. *Science* 170: 593-598.
- Herrero, S. 1970c. Man and the grizzly bear (past, present, but future?). *Bio Science* 20(21): 1148-1153.
- Herrero, S. (Editor). 1972a. *Bears: Their Biology and Management*. New Series #23, International Union for Conservation of Nature, Morges, Switzerland.
- Herrero, S. 1972b. Aspects of evolution and adaptation in American black bears (*Ursus americanus* Pallus) and brown and grizzly bears (*U. arctos* Linne) of North America. Pp. 221-231, In: S. Herrero (Ed.), *Bears--Their Biology and Management* New Series #23, International

- Union for Conservation of Nature, Morges, Switzerland.
- Herrero, S. 1976. Conflicts between man and grizzly bears in the National Parks of North America. Pp. 121-145, In: M. Pelton, J. W. Lentfer, and G. E. Folk (Eds.), *Bears--Their Biology and Management*, New Series #40, International Union for Conservation of Nature, Morges, Switzerland.
- Herrero, S. 1977. Black bears: The grizzlies' replacement? Paper delivered to Black Bear Workshop, sponsored by the Boone & Crockett Club, Feb. 1977, Kalispell, Montana (proceedings also in press).
- Herrero, S., and D. Hamer. 1977. Courtship and copulation of a pair of grizzly bears--with comments on reproductive plasticity and strategy. *Journal of Mammalogy* 58(3): 441-444.
- Hornocker, M. G. 1962. Population characteristics and social and reproductive behavior of the grizzly bear in Yellowstone National Park. MS Thesis, Montana State University, Missoula.
- Jonkel, C., and I. McTaggart Cowan. 1971. The black bear in the spruce-fir forest. *Wildlife Monograph* 24: 57 pp.
- Lindzey, F. 1976. Black bear population ecology. PhD. Thesis. Oregon State University, Corvallis.
- Kemp, G. A. 1976. The dynamics and regulation of black bear, *Ursus americanus*, populations in Northern Alberta. Pp. ---, In: M. R. Pelton, J. W. Lentfer and G. E. Folk (Eds.), *Bears--Their Biology and Management*, New Series #40, International Union for Conservation of Nature, Morges, Switzerland, 467 pp.
- Krott, P., and Krott, G. 1962. Zum Verhalten des braun baren (*Ursus arctos* L. 1758) in den Alpen. *Zeitschrift für Tierpsychologie* 20: 160-206.
- Martinka, C. 1973. Interim report on grizzly bear research. U.S. Government memo dated Oct. 25, 1975, Glacier National Park, U.S.A.
- Martinka, C. J. (Editor). *Proceedings of the Fourth International Conference on Bear Research and Management*.
- Mealey, S. P. 1975. The natural food habits of free ranging grizzly bears in Yellowstone National Park, 1973-1974. MSc Thesis, Montana State University, Bozeman.
- Mundy, K. 1963. Ecology of the grizzly bear (*Ursus arctos*) in Glacier National Park, British Columbia. MSc Thesis, University of Alberta, Edmonton.
- Murie, A. 1944. *The Wolves of Mt. McKinley*. Fauna Series #5. U.S. Dept. of the Interior, Washington, D.C.
- Murie, A. 1963. *A Naturalist in Alaska*. Doubleday Anchor Books, Garden City, New York.
- Pearson, A. 1975. The northern interior grizzly bear (*Ursus arctos* L.). Canadian Wildlife Service, Report Series #34: 84 pp.
- Pearson, A. M. (Editor). 1968. *Proceedings of the First Bear Workshop*. Whitehorse, Yukon. Canadian Wildlife Service, Edmonton.
- Pelton, M. R., and G. M. Burghardt. 1976. Black bears of the Smokies. *Natural History* 85(1): 54-63.
- Pelton, M. R., J. W. Lentfer, and G. E. Folk (Editors). 1976. *Bears--Their Biology and Management*. New Series #40, International Union for Conservation of Nature, Morges, Switzerland.
- Poelker, R. J., and H. D. Hartwell. 1973. *Black Bears of Washington*. Washington State Game Department Biological Bulletin 14: 149 pp.
- Reynolds, D., and J. Beecham. 1977. Home range activities and reproduction of black bears in west-central Idaho. Paper delivered to Fourth International Conference on Bear Research and Management, Feb. 21-24, Kalispell, Montana.
- Rogers, L. 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. *Transaction of North American Wildlife and Natural Resources Conference* 41: 431-438.
- Rogers, L. 1977. Movements and social relationships of black bears in northeastern Minnesota. PhD Dissertation, University of Minnesota, St. Paul.
- Schaller, G. B. 1972. *The Serengeti Lion: A Study of Predator-prey Relations*. University of Chicago Press, Chicago.
- Shaffer, S. C. 1971. Some ecological relationships of grizzly bears and black bears of the Apgar Mountains in Glacier National Park, Montana. MSc Thesis, University of Montana, Missoula.
- Stonorov, D., and A. W. Stokes. 1972. Social behavior of the Alaska brown bear. Pp. 232-242, In: S. Herrero (Ed.), *Bears--Their Biology and Management*. New Series #23, International Union for Conservation of Nature, Morges, Switzerland.
- Sugiyama, Y. 1967. Social organization of hanuman langurs. Pp. 221-236, In: S. A. Altman (Ed.), *Social Communication Among Primates*. University of Chicago Press.
- Tisch, E. L. 1961. Seasonal food habits of the black bear in the Whitefish Range of Northwestern Montana. MSc Thesis, Montana State University, Bozeman.
- Troyer, W. A., and R. J. Hensel. 1962. Cannibalism in brown bear. *Animal Behaviour* 10 (3-4): 231 pp.
- Troyer, W. A., and R. J. Hensel. 1964. Structure and distribution of a Kodiak bear population. *Journal of Wildlife Management* 28: 769-772.

REPRODUCTION AND SOCIAL ORGANIZATION OF LIONS FROM THE KRUGER NATIONAL PARK

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Abstract. Reproduction in male and female lions from the Kruger National Park is examined by utilizing material taken from cropped animals and observations made in the field. Subadult males emigrate from the parent group between 27 and 36 17

Errata: CARNIVORE Volume I Part 1 and Part 2.

Part 1: add the following references to Herrero's article, A comparison of Some Features of the Evolution, Ecology and Behavior of Black and Grizzly/Brown Bears, pages 7 - 17.

ADDITIONAL REFERENCES

Collins, J. M. 1973. Some aspects of reproduction and age structures in the black bear in North Carolina. *Proceedings of the Annual Conference of South East Association of Game and Fish Commissioners* 27: 163-170.

Harlow, R. F. 1961. Characteristics and status of the Florida black bear. *Transactions of North American Wildlife and Natural Resources Conference* 26: 481-495.

Hatler, D. F. 1967. Some aspects in the ecology of the black bear (*Ursus americanus*) in Interior Alaska. M. Sc. thesis, University of Alaska, Fairbanks.

Spencer, H. E. Jr. 1955. The black bear and and its status in Maine. *Game Division Bulletin Number 4*: 55pp. State of Maine.

Stickley, A. R. 1961. A black bear tagging study in Virginia. *Proceedings of the Annual Conference of South East Association of Game and Fish Commissioners* 15: 43-54.

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